

Genetic relationships of some *Gazella* species: an allozyme survey

By M. VASSART, L. GRANJON, A. GRETH, and F. M. CATZEFLIS

Ecole Nationale Vétérinaire de Toulouse, Toulouse, France; Museum National d'Histoire Naturelle, Paris, France; National Wildlife Research Center, Taif, Saudi Arabia; and Institut des Sciences de l'Evolution, Université de Montpellier II, Montpellier, France

Receipt of Ms. 22. 11. 1993
Acceptance of Ms. 17. 1. 1994

Abstract

An allozyme comparison of eight taxa in the genus *Gazella* (Bovidae: Artiodactyla) was conducted to clarify the systematic relationships of endangered gazelles currently bred in Saudi Arabia for reintroduction. Electrophoretic variation at 16 genetic loci suggested that several similar taxa of Arabian gazelles, namely *G. gazella gazella*, *G. gazella erlangeri*, *G. gazella farasani*, and *G. gazella cora*, belong to the same species of *G. gazella* sensu lato. Four other species proved to have diverged genetically: *G. thomsoni* and *G. dorcas*, which cluster together, *G. rufifrons*, and *G. subgutturosa*. The subgenus *Trachelocele*, in which the latter species has been placed according to morphological characteristics, is not supported. Polymorphism and heterozygosity values found in *Gazella* were generally similar to average values reported for mammals. The results are discussed in terms of the strategy to follow a conservation program that take genetic data into account.

Introduction

There is urgent need for conservation action concerning gazelles (RYDER 1987), both in captive and wild populations. Of the 12 species of *Gazella* (CORBET and HILL 1980), nine are considered vulnerable or endangered (IUCN 1988), mainly due to overhunting and habitat destruction. In Saudi Arabia, where at least three "good biological species" (MAYR 1963) are found: *G. saudiya*, *G. subgutturosa* and *G. gazella* (see Fig. 1), the situation is of particular concern (THOULESS et al. 1991). Over the last few years, tremendous efforts have been undertaken towards the conservation of gazelles in this country (ABU-ZINADA et al. 1989). It is widely accepted that species conservation must be based on proper systematics of the endangered taxa (RYDER 1986; GROVES 1988).

Morphological characters such as size and shape of horns and skull have been previously used to establish systematics in *Gazella* (GROVES 1969, 1983; LANGE 1972; GROVES and LAY 1985; ALADOS 1986/1987). Color and coat patterns have also been used, but these characters may vary due to environmental conditions (HARRISON and BATES 1991; GROVES and LAY 1985). Cytotaxonomy seems to be particularly informative, and can be helpful in characterizing some species, as the Indian-gazelle, *G. bennetti* (FURLEY et al. 1988). Up to now, only limited data on the genetic diversity in the genus *Gazella* are available based on protein electrophoresis (TEMPLETON et al. 1987; GRANJON et al. 1991). This technique has proven to be useful in a number of studies both for captive breeding management purposes (see WAYNE et al. 1986) and for systematic and phylogenetic studies (see BUTH 1984 for a review). Advocating a phylogenetic basis for taxonomy, including subspecies groupings (see CRACRAFT 1989 for a discussion of the phylogenetic species concept), the present study shows the results of allozyme variation in eight taxa of gazelles and proposes some hypotheses on the phylogeny and conservation of this group.

In particular the following questions were posed: 1. Among the three species present in

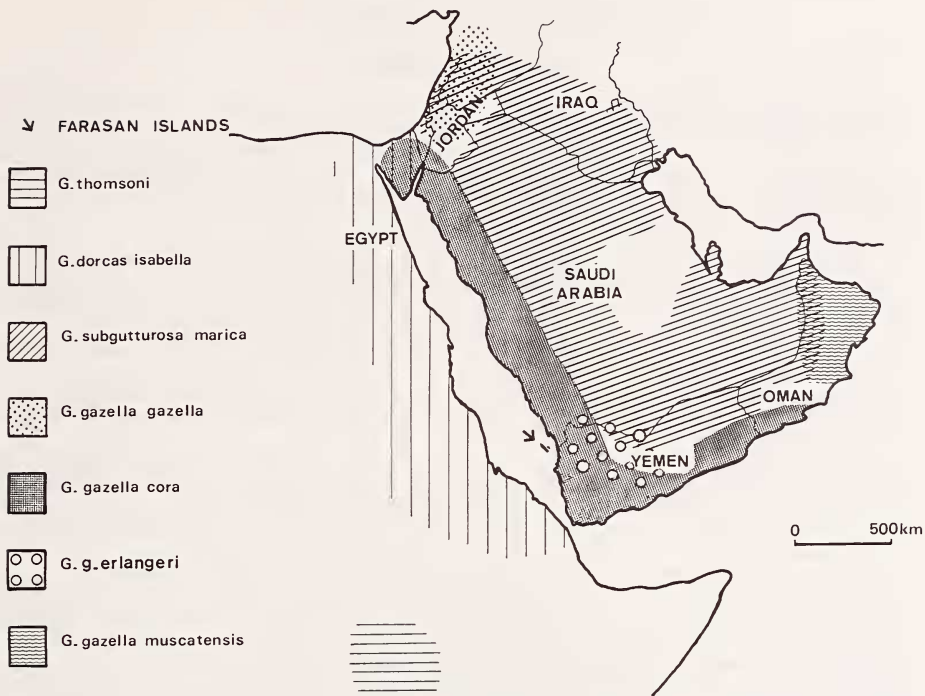


Fig. 1. Distribution of eight taxa of *Gazella* in the Arabian peninsula and in East Africa. On Farasan Islands lives *G. g. farasani*. Areas of sympatry for *G. g. gazella* and *G. g. cora*, *G. g. cora* and *G. g. erlangeri* are tentative. Data from GROVES (1985), DORST and DANDELLOT (1972), HARRISON and BATES (1991) and KINGSWOOD and KUMAMOTO (1988)

Saudi Arabia, *G. subgutturosa* has been considered very divergent morphologically from all other members of the genus, and placed alone in the subgenus *Trachelocele* (ELLERMAN and MORRISON-SCOTT 1951). Is this morphological divergence accompanied by significant molecular genetic divergence? 2. GROVES (1983) proposed that the insular gazelles living on the Farasan Islands in the Red Sea should be treated as a separate species, namely *G. arabica*. However, GROVES (1989) pointed out that *G. arabica* resembles *G. gazella* more closely than any other species. Based on skull measurements, THOULESS and AL BASRI (1991) proposed to consider gazelles from the Farasan islands as a subspecies of *G. gazella*, named *G. g. farasani*. Are electrophoretic data able to help differentiate between these two hypotheses? 3. At least five subspecies have been attributed to *Gazella gazella* sensu lato: *G. g. muscatensis*, *G. g. gazella*, *G. g. cora*, *G. g. farasani* and *G. g. erlangeri* (GROVES 1989; THOULESS and AL BASRI 1991; GROVES et al. 1994) based on morphological characteristics. Do some fixed allelic differences characterize any of these taxa, hence supporting the concept of separate gene pools in *G. gazella* sensu lato? 4. The taxonomic position of *G. rufifrons* is not clear. GROVES (1975, 1985, 1988) described the Red-fronted Gazelle *G. rufifrons* with 7 subspecies: *rufifrons*, *laevipes*, *kanuri*, *tilonura*, *albonotata*, *nasalis* and *thomsoni*. The last three subspecies have usually been grouped in a different species: *G. thomsoni* (DORST and DANDELLOT 1972; CORBET and HILL 1980; NOWAK and PARADISO 1983). Is *G. thomsoni* a subspecies of *G. rufifrons*?

To address these questions, we have analysed by means of protein electrophoresis, samples of gazelle species from the Arabian peninsula, and 3 African species.

Material and methods

Origin of the animals

Gazella thomsoni albonotata (n = 8): eight animals from private collections in Saudi Arabia, all originating from Sudan. This taxon is called *G. rufifrons albonotata* by GROVES (1985, 1988).

Gazella dorcas (n = 25): 16 individuals from different private collections in Saudi Arabia, 5 from Taif breeding center (National Wildlife Research Center, Saudi Arabia), and 4 from Thumama breeding center (King Khaled Wildlife Research Center, Saudi Arabia). The probable origin for all is Sudan. These animals would be representative of the taxon *G. dorcas isabella* mentioned by GROVES (1969) and ALADOS (1986/1987).

Gazella subgutturosa (n = 30): 30 animals from Thumama center. They represent the subspecies *G. s. marica* (NADER 1989). This species is endangered (IUCN 1988) and limited to a very small geographic area in the Arabian peninsula, but is still common in Mongolia and in some parts of Russia (GROVES 1988).

Gazella gazella gazella (n = 16): 16 individuals from the Thumama center. This gazelle is locally abundant in Northern Israel.

Gazella gazella cora (n = 7): 5 animals from Taif center and 2 from a private Saudi collection; they may have originated in Saudi Arabia. *G. g. cora* is rare and endangered in the mountains east of the Red Sea (GROVES 1988).

Gazella gazella farasani (n = 5). 4 individuals from a private collection on Farasan Kebir island (Red Sea) and 1 wild gazelle from Farasan Kebir island. This taxon, distributed on Farasan islands, was previously called *G. arabica* by GROVES (1985) but is more probably a subspecies of *G. gazella* (THOULESS and AL BASRI 1991). Its population status has been recently examined by FLAMAND et al. (1988), who found that these gazelles were still present in fairly large numbers.

Gazella gazella erlangeri (n = 15): 6 animals from Taif center, some of them thought to have been caught in the South of Saudi Arabia, 5 animals held in private collections in Saudi Arabia, 4 individuals from a pet shop in Djeddah. For the latter samples the origin was reported to be the region of Aden (Yemen). This subspecies has recently been described by GROVES et al. (1994) after morphological and skull measurement comparisons with *G. g. cora* and *G. g. muscatensis*.

Gazella rufifrons (n = 1): 1 specimen from a private collection in Saudi Arabia. The origin of this sample is unknown. This gazelle could belong to the subspecies *kanuri* (synonym = *centralis*) or *laevipes* (synonym = *hasleri*) which are very similar.

Electrophoresis

Horizontal starch gel electrophoresis was performed on blood extracts collected by jugular puncture. An isotonic saline solution was added to the samples, and the plasma was separated from the red blood cells by centrifugation. Samples were duplicated for a reference collection and stored at -30°C until electrophoresis was performed.

Electrophoresis, staining of the proteins, and scoring the results were conducted according to PASTEUR et al. (1988). Many allozyme systems were assayed under different electrophoretic conditions, but only 16 loci that gave consistent results were retained (Tab. 1). Statistical and phylogenetic treatments were performed without taking hemoglobin into account, as the A and B subunits were not separated before running the gels. This prevented us from scoring the different alleles. Nevertheless, haemoglobin pattern appears very useful to distinguish *G. subgutturosa* as will be discussed further.

For each taxon, the percentage of polymorphic loci (P 95 %, i.e. a locus is considered polymorphic when the frequency of the most common allele is not higher than 0.95), mean number of alleles per locus (A), and mean heterozygosity (H) were calculated. Genetic distances between samples were estimated using formulae from NEI, "unbiased minimum distance" (1978) and ROGERS (1972). The Arabian oryx (*Oryx leucoryx*) was used as an outgroup to root the tree for a phenetic analysis, with only 14 loci, because MPI and ACP could not be scored in this species. Allelic frequencies for Arabian oryx were published by VASSART et al. (1991). Phenetic analysis was performed via the Distance Wagner method (in BIOSYS-1, SWOFFORD and SELANDER 1989), using the ROGERS distance (1972) as modified by WRIGHT (1978).

For cladistic analysis, allelic frequencies were coded as „locus-as-character“ (see BUTH 1984). Alleles with low frequencies were kept even though this might have introduced a bias for small sample sizes. Data for oryx were not used here, as the information they bring after coding was too weak. Cladistic analysis was performed using PAUP 3.0 (SWOFFORD 1990). Unordered option was used, and the consensus tree obtained with branch-and bound search after 1000 bootstrap replications was finally retained (threshold of 95 %).

Table 1. Enzymes surveyed and electrophoretic buffers used

Enzymes	Tissue	Locus	Buffer (pH)
GOT: Aspartate aminotransferase (EC 2.6.1.1)	RBC	1	TME 6.9/6.9
ACP: Acid phosphatase (EC 3.1.3.2)	RBC	1	TC 6.4/6.0
DIA: Diaphorase (EC 1.6.4.3)	RBC	1	TC 6.4/6.0
ES 10-14: Esterase 10 and 14 (EC 3.1.1.X)	RBC	2	TME 6.9/6.9
GLO: Glyoxalase (EC 4.4.1.5)	RBC	1	TBE 8.6/8.6
GPI: Glucose phosphate isomerase (EC 5.3.1.9)	RBC	1	TC 6.4/6.0
LDH: Lactate dehydrogenase (EC 1.1.1.27)	RBC	1	TC 6.4/6.0
MDH: Malate dehydrogenase (EC 1.1.1.37)	RBC	1	TC 6.4/6.0
MOD: Malic enzyme (EC 1.1.1.40)	RBC	1	TC 6.4/6.0
MPI: Mannose phosphate isomerase (EC 5.3.1.8)	RBC	1	TC 6.4/6.0
NP: Nucleoside phosphorylase (EC 2.4.2.1)	RBC	1	TME 6.9/6.9
IPO: Superoxide dismutase (EC 1.15.1.1)	RBC	1	TC 6.4/6.0
ALB: Albumin	Serum	1	LiOH 8.3/8.1
ES 1: Esterase 1 (EC 3.1.1.X)	Serum	1	LiOH 8.3/8.1
TRF: Transferrin	Serum	1	LiOH 8.3/8.1

TME = Tris Maleate, TC = Tris Citrate, TBE = Tris Borate EDTA, LiOH = Lithium Hydroxyde.

Results

Among the 8 *Gazella* taxa, 8 loci were found to be polymorphic; mean heterozygosities (H) varied from 0 to 0.085, mean numbers of alleles per locus (A) from 1.0 to 1.31, and percentages of polymorphic loci (P) from 0 to 18.7 (Tab. 2). Of the eight polymorphic loci, only four exhibited significant variability: ES14, MOD, NP, and TRF (Tab. 2). NP with three alleles was polymorphic in five of seven taxa. ROGERS (and NEI) genetic distances (Tab. 3) varied from 0.012 (0.001) to 0.304 (0.322) among taxa. IPO showed a fixed allelic difference between *G. thomsoni*, *G. dorcas* and *G. rufifrons*, on the one hand, and the five other taxa, on the other. GOT, DIA and GPI displayed minor variation, with a rare (less than 5 % frequency) allele in only one taxon each.

According to phenetic analysis using the Wagner method (Fig. 2), *G. subgutturosa* clusters together with the 4 samples of *G. gazella* sensu lato, and appears more similar to *G. g. erlangeri* mainly due to similar allelic frequencies at the NP locus. When hemoglobin data are considered, all *G. subgutturosa* samples had a unique pattern which distinguishes that species from all others (Fig. 4). On the phenogram, *G. rufifrons* lies in an intermediate position between *G. dorcas*/*G. thomsoni* and the cluster of *G. gazella*/*G. subgutturosa*.

For cladistic analysis, allelic frequencies were coded according to the qualitative method described in BUTH (1984) (Tab. 4). The unrooted cladogram obtained after parsimony analysis (Fig. 3) confirms to a large extent the picture obtained with the phenetic analysis. Most of the samples in the *G. gazella*/*G. subgutturosa* group are characterized by minor autapomorphies (corresponding to low frequency alleles). *G. rufifrons* and the pair *G. dorcas*/*G. thomsoni* are clearly distinguishable from each other and from the *G. gazella*/*G. subgutturosa* group. Two synapomorphies separate *G. rufifrons* from each of the other two clusters.

Discussion

These results raise two points that require further discussion: the systematic implications of these allozyme data, and their implications for the conservation biology of the Arabian gazelles. It should be kept in mind that all the samples used here came from captive

Table 2. Allelic frequencies for variable loci in 8 samples of *Gazella*

Locus	Allele	<i>G. thomsoni</i> (N = 8)	<i>G. dorcas</i> (N = 25)	<i>G. rufifrons</i> (N = 1)	<i>G. subgutturosa</i> (N = 30)	<i>G. g. gazella</i> (N = 16)	<i>G. g. cora</i> (N = 7)	<i>G. g. farasani</i> (N = 5)	<i>G. g. erlangeri</i> (N = 15)	<i>O. leucoryx</i>
GOT	80	1.00	1.00	1.00	1.00	0.03	1.00	1.00	1.00	1.00
	100					0.97				
	120									
DIA	80	1.00	0.02	1.00	1.00	1.00	1.0	1.00	1.00	1.00
	100		0.98							
	120									
ES 14	90									
	100	0.37	0.36		1.00	1.00	1.00	1.00	1.00	1.00
	105	0.63	0.64	1.00						1.00
GPI	80	1.00	1.00	1.00	0.95	1.00	1.00	1.00	1.00	1.00
	100				0.05					
	120									
MOD	90									
	100	0.37	0.32	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	110	0.63	0.68							
NP	60									
	100		0.90	1.00	0.90	0.25	0.07	0.40	1.00	1.00
	120	1.00	0.10		0.10	0.75	0.93	0.60		
IPO	30	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	100									
	120									
TRF	90	0.12	0.96							1.00
	100	0.12	0.04	1.00	0.97	1.00	1.00	1.00	1.00	1.00
	110	0.76			0.03					
H% A		8.5	7.4	—	2.1	2.7	0.8	3.0	0.0	
		1.25	1.31	—	1.19	1.12	1.06	1.06	1.00	
		18.7	18.7	—	12.5	6.2	6.2	6.2	0.0	

N = sample size; H = mean heterozygosity; A = mean number of alleles per locus; P 95% = proportion of polymorphic loci.

populations, often derived from a few individuals, and therefore have probably been subject to sampling effect and subsequent inbreeding and genetic drift. Thus, they may not reflect allele frequencies of the parental populations and the results inferred from these samples should be taken with caution. Unfortunately, it is difficult to correct for these biases because the captive history of these samples is not well documented.

Our allozyme analysis does not support *G. subgutturosa* as an isolated taxon in the genus *Gazella*, or the concept of the subgenus *Tracheloceles* for this species. This is in contradiction to the relationships suggested by ELLERMAN and MORRISON-SCOTT (1951), HALTENORTH (1963), and GROVES (1969). Rather, *G. subgutturosa* appears to be related to *Gazella gazella* sensu lato. Among the protein systems considered here, hemoglobin appears to represent the only discriminative one between these two taxa (see Fig. 4).

The clustering of *G. thomsoni* and *G. dorcas* in the cladistic analysis (2 synapomorphies represented by ES14 and MOD) is surprising, since this was never suggested by studies of comparative morphology. From our data it is difficult to support the view of GROVES (1975, 1985, 1988) or LANGE (1972), who described *G. thomsoni* as a subspecies of *G. rufifrons*. However, chromosome numbers (58) also appear identical in *G. thomsoni* and *G. rufifrons* (VASSART, unpubl. results). Considering allelic frequency (see ES14) *G. rufifrons* could belong to the *G. thomsoni* group, but with a single specimen for *G. rufifrons*, this conclusion would be speculative.

There are no standard levels of genetic divergence associated with subspecies or species rank (see examples in LINNELL and CROSS 1991 and references in CRACRAFT 1989). However, our results suggest that several Arabian gazelles do belong to *Gazella gazella* sensu lato, namely, *G. g. erlangeri*, *G. g. farasani*, *G. g. gazella*, and *G. g. cora*. The small genetic distances between them are not larger than those found between geographic samples in other ungulates (see, for instance, HARTL and REIMOSER 1988; HARTL et al. 1990). The position of *G. g. cora* well inside the *G. gazella* group does not agree with the hypothesis of *G. g. cora* being the Arabian representative of *G. dorcas* (GROVES 1988). This has been confirmed by cytogenetic results: *G. g. cora*, *G. g. gazella*, *G. g. erlangeri* and *G. g. farasani* have 35 chromosomes in males and 34 in females (VASSART et al. 1993) whereas *G. dorcas* have 31 chromosomes in males and 30 in females.

Also, and contrary to the hypothesis of GROVES (1985) and GROVES and LAY (1985), *G. arabica* (our *G.*

Table 3. Rogers (above diagonal) and Nei's (below diagonal) genetic distances between 8 taxa of *Gazella*, and *Oryx leucoryx*

	<i>G. subgutturosa</i>	<i>G. dorcas</i>	<i>G. g. gazella</i>	<i>G. g. farasani</i>	<i>G. g. erlangeri</i>	<i>G. thomsoni</i>	<i>G. g. cora</i>	<i>G. rufifrons</i>	<i>O. leucoryx</i>
<i>G. subgutturosa</i>	—								
<i>G. dorcas</i>	0.254	—							
<i>G. g. gazella</i>	0.030	0.245	—						
<i>G. g. farasani</i>	0.016	0.240	0.000	—					
<i>G. g. erlangeri</i>	0.001	0.264	0.040	0.024	—				
<i>G. thomsoni</i>	0.226	0.099	0.176	0.182	0.243	—			
<i>G. g. cora</i>	0.049	0.252	0.001	0.005	0.061	0.172	—		
<i>G. rufifrons</i>	0.201	0.165	0.147	0.152	0.214	0.083	0.143	—	
<i>O. leucoryx</i>	0.704	0.540	0.700	0.697	0.716	0.656	0.711	0.716	—

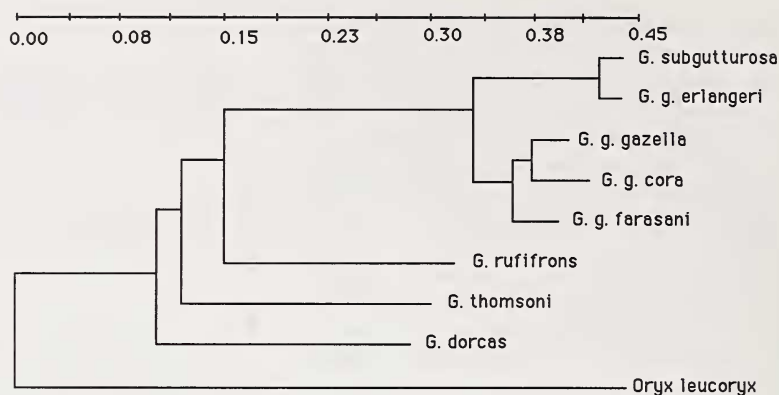


Fig. 2. Dendrogram derived from the WAGNER procedure on the matrix of ROGERS genetic distances

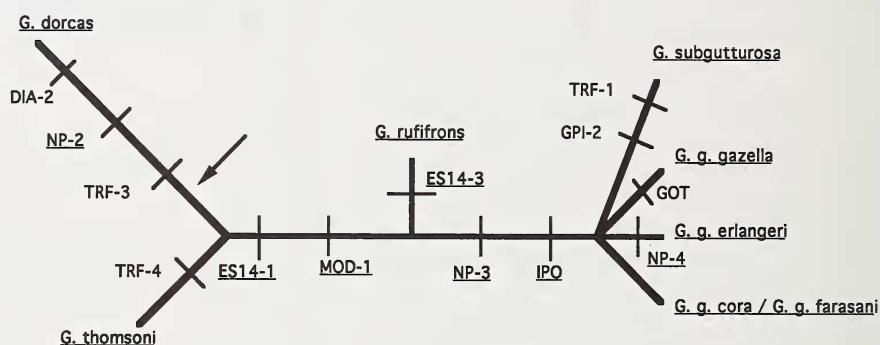


Fig. 3. Cladogram obtained with "locus as character" coding using branch-and-bound search after 1000 bootstrap replications. Synapomorphies are underlined, other characters are autapomorphies. The arrow points to the root leading to the outgroup (see Fig. 2)

Table 4. Qualitative coding of allelic presence in sample data set from table 2

See text for explanations

	GOT	DIA	ES14	GPI	MOD	NP	IPO	TRF
<i>G. thomsoni</i>	1	1	2	1	2	1	2	4
<i>G. dorcas</i>	1	2	2	1	2	2	2	3
<i>G. rufifrons</i>	1	1	3	1	1	1	2	2
<i>G. subgutturosa</i>	1	1	1	2	1	3	1	1
<i>G. g. gazella</i>	2	1	1	1	1	3	1	2
<i>G. g. cora</i>	1	1	1	1	1	3	1	2
<i>G. g. farasani</i>	1	1	1	1	1	3	1	2
<i>G. g. erlangeri</i>	1	1	1	1	1	4	1	2

g. farasani) should not be treated as a different species, but as a morphological and/or geographical race or subspecies of *G. gazella*: *G. g. farasani* as proposed by THOULESS and AL BASRI (1991).

As stated by FURLEY et al. (1988: page 48), "no common agreement has yet been reached on the number of genuine species within [*Gazella*]. . .", because of the considerable morphological variation shown by some species and the possibility of morphological



Fig. 4. Hemoglobin gel with TBE 8.6/8.6 buffer: R; *G. subgutturosa*, G; *G. gazella*, T; *G. thomsoni*. *G. dorcas* has the same patterns as *G. gazella*

convergence between taxa as illustrated by the cladistic analysis of skull and jaw characters of ALADOS (1986/1987). For this reason, we feel that a non-morphological approach, such as allozyme electrophoresis, should be used for reconstructing the systematics and evolutionary relationships of the gazelles. Examination of other species in the genus is needed, as well as the scoring of a greater number of loci.

With respect to conservation issues, GROVES (1989) stated that „for conservation purposes it is quite clear that each of the Arabian forms [*G. subgutturosa marica*, *G. gazella cora* and *G. dorcas saudiya*] represents a unique gene pool.” Our data on the former two species support this view. But, as far as local forms are concerned, we have to deal with the “dilemma of subspecies” (RYDER 1986) when considering *G. g. gazella*, *G. g. cora*, *G. g. farasani*, and *G. g. erlangeri*. On the basis of our results, they are genetically very similar, however, from a conservation biologist’s point of view, they might represent “unique gene pools,” each one of which adapted to a particular local environment.

Among the different guidelines entering into consideration for selecting wild animals to be used for breeding purposes, genetic parameters such as mean heterozygosity and percentage of polymorphic loci should be taken into account. The data derived from our samples of *Gazella* (see Tab. 2) are similar to those found in natural populations of artiodactyls (see BACCUS et al. 1983; VASSART et al. 1991, for reviews). The mean heterozygosity for 184 species of mammals is 4.1 % (± 3.5 SD) (NEVO et al. 1984), a value similar to the one observed for the three *Gazella* samples represented by more than 10 individuals in our study. On the other hand, the absence of genetic variability (despite the different origins of the samples) for *G. g. erlangeri* is potentially problematic. This gazelle is only known from captive individuals and there is no protected area on its supposed range (southwest of the Arabian peninsula). It is possible that the lack of polymorphism and heterozygosity resulted from the population bottleneck experienced by this subspecies. This could lead to inbreeding problems (O’BRIEN et al. 1983).

These results have to be confirmed by other molecular techniques such as mitochondrial DNA sequencing. This phylogenetic tool could be useful to differentiate all the different species of gazelles even if they are of recent origin, but could be of limited value at the subspecific level (CRONIN 1992).

Acknowledgements

This work was carried out under the patronage of HRH Prince SAUD AL FAISAL and Dr. ABUZINADA, Secretary of the National Commission for Wildlife Conservation and Development of the Kingdom of Saudi Arabia. The technical help of J.-F. AGNÈSE, G. BERREBI and L. DURAND during the establishment of the laboratory experiments has been invaluable. We wish to express our thanks to two anonymous reviewers and to M. A. CRONIN who provided valuable comments on the manuscript. We thank J. F. VOISIN for help in translating the summary into German. This is contribution 94-014 of the Institut des Sciences de l’Evolution (Montpellier, France).

Zusammenfassung

Genetische Verwandtschaft einiger Gazella-Arten: Eine Allozym-Untersuchung

Acht Arten der Gattung *Gazella* (Bovidae: Artiodactyla) wurden mit einer Allozymanalyse verglichen, um die genetische Verwandtschaft von Gazellen zu überprüfen, die derzeit in Saudi-Arabien zur Wiedereinbürgerung gezüchtet werden. Die elektrophoretische Untersuchung von 16 polymorphen Loci deutet darauf hin, daß mehrere ähnliche Taxa, nämlich *G. gazella gazella*, *G. gazella erlangeri*, *G. gazella farasani* und *G. gazella cora* zur gleichen Art *G. gazella* sensu lato gehören. Vier andere Arten sind davon deutlich genetisch verschieden: *G. thomsoni* und *G. dorcas*, die genetisch ähnlich sind, sowie *G. rufifrons* und *G. subgutturosa*. Die Untergattung *Trachelocele*, der die letzte Art aufgrund morphologischer Merkmale zugeordnet worden ist, konnte aufgrund der Allozymvergleiche nicht bestätigt werden. Die Polymorphismus- und Heterozygotie-Grade der Gattung *Gazella* waren insgesamt den bei anderen Säugern gefundenen Werten ähnlich. Die Ergebnisse werden im Hinblick darauf diskutiert, welche Schlußfolgerungen sich aus den genetischen Untersuchungen für ein angestrebtes Schutzprogramm ergeben.

References

- INTERNATIONAL UNION FOR CONSERVATION OF NATURE (1988): Red list of threatened animals. Gland, Switzerland: IUCN.
- ABU-ZINADA, A. H.; GORIUP, P. D.; NADER, I. A. (1989): Wildlife conservation and development in Saudi Arabia. Riyadh: NCWCD.
- ALADOS, C. L. (1986/1987): A cladistic approach to the taxonomy of the Dorcas gazelles. *Isr. J. Zool.* **34**, 33–49.
- BACCUS, R.; RYMAN, N.; SMITH, M. H.; REUTERWALL, C.; CAMERON, D. (1983): Genetic variability and differentiation of large grazing mammals. *J. Mammalogy* **64**, 109–120.
- BUTH, D. G. (1984): The application of electrophoretic data in systematic studies. *Ann. Rev. Ecol. Syst.* **15**, 501–522.
- CORBET, G. B.; HILL, J. E. (1980): A world list of Mammalian Species. London: British Museum; Comstock Publishing Ass. Cornell University Press.
- CRACRAFT, J. (1989): Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In: Speciation and its consequences. Ed. by D. OTTE and J. A. ENDLER. Sunderland, Massachusetts: Sinauer Ass. Pp. 28–59.
- CRONIN, M. A. (1992): Intraspecific variation in mitochondrial DNA of north American cervids. *J. Mammalogy* **73**, 70–82.
- DORST, J.; DANDELLOT, P. (1972): A field guide of larger mammals of Africa. London: Collins.
- EFFRON, M.; BOGART, H.; KUMAMOTO, A. T.; BENIRSCHKE, K. (1967): Chromosome studies in the mammalian subfamily Antilopinae. *Genetica* **46**, 419–444.
- ELLERMAN, J. R.; MORRISON-SCOTT, T. C. S. (1951): Checklist of Palearctic and Indian mammals 1758 to 1946. London: British Museum (Natural History).
- FLAMAND, J. R. B.; THOULESS, C. R.; TATWANY, H.; ASMODÉ, J. F. (1988): Status of the gazelles of the Farasan Islands, Saudi Arabia. *Mammalia* **52**, 608–610.
- FURLEY, C. W.; TICHY, H.; UERPMANN, H. P. (1988): Systematics and chromosomes of the Indian gazelle *Gazella bennetti* (Sykes, 1831). *Z. Säugetierkunde* **53**, 48–54.
- GRANJON, L.; VASSART, M.; GRETH, A. (1991): Genetic study of Sand gazelles from Saudi Arabia; chromosomal and isozymic data. *Z. Säugetierkunde* **56**, 169–176.
- GROVES, C. P. (1969): On the smaller gazelles of the genus *Gazella* Blainville, 1816. *Z. Säugetierkunde* **34**, 38–60.
- (1975): Notes on the gazelles. *Gazella rufifrons* and the zoogeography of Central African Bovidae. *Z. Säugetierkunde* **40**, 308–319.
- (1983): Notes on the gazelles. IV. The Arabian gazelles collected by Hemprich and Ehrenberg. *Z. Säugetierkunde* **48**, 371–381.
- (1985): An introduction to the gazelles. *Chinkara* **1**, 4–16.
- (1988): A catalogue of the genus *Gazella*. In: Conservation and biology of desert antelopes. Ed. by A. DIXON and D. JONES. London: C. Helm. Pp. 193–198.
- (1989): The gazelles of the Arabian peninsula. In: Wildlife conservation and development in Saudi Arabia. Ed. by A. H. ABU-ZINADA, P. D. GORIUP, and I. A. NADER. Riyadh: NCWCD. Pp. 237–248.
- GROVES, C. P.; LAY, D. M. (1985): A new species of the genus *Gazella* (Mammalia: Artiodactyla: Bovidae) from the Arabian peninsula. *Mammalia* **49**, 27–36.
- GROVES, C. P.; THOULESS, C.; VASSART, M. (1994): Subspecies of *Gazella gazella* in Saudi Arabia. Fauna of Saudi Arabia (in prep.)
- HALTENORTH, T. (1963): Klassifikation der Säugetiere: Artiodactyla. *Hdb. Zool.* **32**, 1–167.
- HARRIS, H.; HOPKINSON, D. A. (1976): Handbook of enzyme electrophoresis in human genetics. Amsterdam: North-Holland.

- HARRISON, D. L.; BATES, P. J. J. (1991): The mammals of Arabia. Sevenoaks, England: Harrison Zool. Museum Publ.
- HARTL, G. B.; REIMOSER, F. (1988): Biochemical variation in roe deer (*Capreolus capreolus* L.): are r-strategists among deer genetically less variable than K-strategists? *Heredity* **60**, 221–227.
- HARTL, G. B.; WILLING, R.; LANG, G.; KLEIN, F.; KÖLLER, J. (1990): Genetic variability and differentiation in red deer (*Cervus elaphus* L.) of Central Europe. *Genet. Sel. Evol.* **22**, 289–306.
- KINGSWOOD, S. C.; KUMAMOTO, A. T. (1988): Research and management of Arabian Sand gazelle in the USA. In: *Conservation and biology of desert antelopes*. Ed. by A. DIXON and D. JONES. London: C. Helm. Pp. 212–226.
- LANGE, J. (1972): Studien an Gazellenschädeln. Ein Beitrag zur Systematik der kleinen Gazellen, *Gazella* (De Blainville, 1816). *Säugetierkd. Mitt.* **20**, 193–249.
- LINNELL, J. C. D.; CROSS, T. F. (1991): The biochemical systematics of red and sika deer (genus *Cervus*) in Ireland. *Heredity* **115**, 267–273.
- MAYR, E. (1963): *Animal species and evolution*. Cambridge: Harvard Univ. Press.
- NADER, I. A. (1989): Rare and endangered mammals of Saudi Arabia. In: *Wildlife conservation and development in Saudi Arabia*. Ed. by A. H. ABU-ZINADA, P. D. GORIUP, and I. A. NADER. Riyadh: NCWCD. Pp. 220–233.
- NEI, M. (1978): Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics*, **89**, 583–590.
- NEVO, E.; BEILES, A.; BEN-SHLOMO, R. (1984): The evolutionary significance of genetic diversity: Ecological, demographic, and life history correlates. In: *Evolutionary dynamics of genetic diversity*. Ed. by G. S. MANI. New York: Springer-Verlag. Pp. 13–213.
- NOWAK, R. M.; PARADISO, J. L. (1983): *Walker's mammals of the world*. London: Johns Hopkins Univ. Press.
- O'BRIEN, S. J.; GOLDMAN, D.; MERRIL, C. R.; BUSH, M. (1983): The cheetah is depauperate in genetic variation. *Science* **221**, 459–462.
- PASTEUR, N.; PASTEUR, G.; BONHOMME, F.; CATALAN, J.; BRITTON-DAVIDIAN, J. (1988): Practical isozyme genetics. Shister, G. B: Ellis Horwood Ltd.
- ROGERS, J. S. (1972): Measures of genetic similarity and genetic distance. *Studies in Genet.* **VII**, Univ. Texas Publ. **7213**, 145–153.
- RYDER, O. A. (1986): Species conservation and systematics: the dilemma of subspecies. *Trends in Ecology and Evolution* **1**, 9–10.
- (1987): Conservation action for gazelles: an urgent need. *Trends in Ecology and Evolution* **2**, 143–144.
- SWOFFORD, D. L. (1990): PAUP: Phylogenetic analysis using parsimony, Version 3.0. Champaign, Illinois: Computer program distributed by the Illinois Natural History Survey.
- SWOFFORD, D. L.; SELANDER, R. B. (1981): BIOSYS-1: A FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. *J. Heredity* **72**, 281–283.
- TEMPLETON, A. R.; DAVIS, S. K.; READ, B. (1987): Genetic variability in a captive herd of speke's gazelle (*Gazella spekei*). *Zoo Biology* **6**, 305–313.
- THOULESS, C. R.; AL BASRI, K. (1991): Taxonomic status of the Farasan Island gazelle. *J. Zool. (London)* **223**, 151–159.
- THOULESS, C. R.; GRAINGER, J. G.; SHOBRAK, M.; HABIBI, K. (1991): Conservation status of gazelles in Saudi Arabia. *Biological Conservation* **58**, 85–98.
- VASSART, M.; GRANJON, L.; GRETH, A. (1991): Genetic variability in the Arabian Oryx. *Zoo Biology* **10**, 399–408.
- VASSART, M.; GRETH, A.; CRIBIU, E. P. (1993): Cytogenetic survey of gazelles from Middle East. X. European Colloquium on Cytogenetics of Domestic Animals, Utrecht. Pp. 253–256.
- WAYNE, R. K.; FORMAN, L.; NEWMAN, A. K.; SIMONSON, J. M.; O'BRIEN, S. J. (1986): Genetic monitors of zoo populations: morphological and electrophoretic assays. *Zoo Biology* **5**, 215–232.
- WRIGHT, S. (1978): *Evolution and the genetics of populations*. Vol 4: Variability within and among natural populations. Chicago, Illinois: University of Chicago Press.

Authors' addresses: MARC VASSART, Ecole Nationale Vétérinaire de Toulouse, 23 chemin des Capelles, F-31076 Toulouse, France; LAURENT GRANJON, Muséum National d'Histoire Naturelle, 55 rue Buffon, F-75005 Paris, France; ARNAUD GRETH, National Wildlife Research Center, P. O. Box 1086, Taif, Saudi Arabia; FRANÇOIS M. CATZEFELIS, Université de Montpellier II, Institut des Sciences de l'Évolution, URA 327 CNRS, F-34095 Montpellier, France